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Isolated theropod teeth from the Middle Jurassic of Niger and the early dental evolution of Spinosauridae

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Four isolated theropod teeth from the ?Bathonian "Argiles de l'Irhazer" in Niger are described. The teeth were found in association with the holotype of the basal sauropod *Spinophorosaurus nigerensis*. These specimens have been assigned to two different taxa by independent analyses, such as direct comparison with teeth previously described in the literature, discriminant and morphometric analyses from metric characters, and cladistic and cluster analyses from discrete characters. The results suggest that three teeth share affinities with those of Megalosauridae and Allosauridae, belonging most likely to the former. The fourth tooth might be from a member of the stem group Spinosauridae. If so, this would be the oldest representative of this clade. This tooth shows a combination of characters that are unusual in typical spinosaurid teeth (crown moderately compressed labiolingually and curved distally with minute denticles on the carina and a deeply veined enamel surface texture without apicobasal ridges). This could shed light on the morphological transition from the plesiomorphic ziphodont dental pattern to that of Spinosauridae. This tooth would also allow a better understanding of the origin of the spinosaurids, supporting a Gondwanan origin for the group.

Key words: Theropoda, Megalosauridae, Spinosauridae, dental morphology, multivariate analyses, Jurassic, Africa.

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Introduction

Spinosaurid theropods are a highly specialized clade of non-avian dinosaurs characterized by crocodile-like skull and teeth (Charig and Milner 1997; Sereno et al. 1998; Sues et al. 2002). Based on their cranial morphology and mechanics (Rayfield et al. 2007), isotope analysis of their remains (Amiot et al. 2010), stomach contents (Charig and Milner 1997), and direct evidence of predation (Buffetaut et al. 2004), spinosaurids are considered to be large, active predators feeding on other dinosaurs, pterosaurs, and fish. Recently, a semiaquatic lifestyle for *Spinosaurus aegyptiacus* has been proposed by Ibrahim et al. (2014) due to the number of aquatic adaptations in the skull, neck, hindlimbs, and pedal claws. As in other dinosaurs, isolated teeth are the most commonly found remains of spinosaurids because of their continuous replacement and the high preservation potential provided by their enamel coating (Currie et al. 1990; Bertin 2010). Spinosaurid teeth show discrete characters (i.e., subconical morphology, minute denticles or unserrated carinae, and deeply veined enamel texture) that allow

their identification with a high degree of certainty (Charig and Milner 1997; Sereno et al. 1998; Canudo et al. 2008; Hendrickx and Mateus 2014). However, non-spinosaurid theropod teeth, with some exceptions (e.g., *Chilesaurus diegosuarezi* Novas et al. 2015 or troodontids Holtz et al. 1998), are difficult to identify with precision because their dental features (i.e., denticle shape or marginal undulations) are plesiomorphic or strongly subjected to homoplasy (Currie et al. 1990; Farlow et al. 1991; Brusatte et al. 2007; see also Hendrickx and Mateus 2014 and Hendrickx et al. 2015 for a more thorough discussion). Over the last decade, morphometric methods have been developed to address this issue. Available databases can be used to assess isolated specimens by means of Discriminant Function Analyses (DFA) or Canonical Variate Analyses (CVA), which yield a good probability of accurate identification (Smith et al. 2005; Smith and Lamanna 2006; Richter et al. 2012; Larson and Currie 2013; see Hendrickx et al. 2015 for a different opinion). Spinosaurids are known from many Cretaceous sites in Africa, South America, Asia, Europe, and Australia (Bertin 2010). However, the record of Jurassic spinosaurids is restricted to two questionable teeth from the Upper Jurassic of Tanzania (Buffetaut 2011; but see also the discussion in Rauhut 2011) and two isolated teeth from the Middle Jurassic of Niger (Serrano-Martínez et al. 2015). The origin and biogeography of this clade is still unclear. It was generally considered that the group dispersed from Laurasia to Africa and, from there, to South America (Buffetaut and Ouaja 2002; Machado and Kellner 2005; Ruiz-Omeñaca et al. 2005). However, recent studies and findings suggest that the dispersal direction is more complex than previously thought (Buffetaut 2011; Allain et al. 2012).

The sequence of changes undergone by the dentition of spinosaurids to acquire its characteristic morphology remains poorly known. On the basis of the two specimens from the Upper Jurassic (?Tithonian) of Tanzania, Buffetaut (2011) described the possible transition of dental morphology from the non-spinosaurid ancestor to early spinosaurids. These teeth show apicobasal ridges, a typical feature of spinosaurid enamel ornamentation, but their shape and the number of denticles are closer to the condition in non-spinosaurid theropods. However, their enamel ornamentation also resembles that of other theropods, such as *Ceratosaurus*, *Paronychodon*, *Zapsalis*, *Acheroraptor*, and *Coelophysis* (Currie et al. 1990; Madsen and Welles 2000; Larson and Currie 2013; Lisa Buckley personal communication 2015), and as such the affinities of these two teeth remain uncertain (Rauhut 2011).

Four theropod teeth were recovered associated with the remains of the holotype of the basal sauropod *Spinophorosaurus nigerensis* Remes et al. 2009, in Agadez, Niger, during the 2007 field campaign of the Palaeontology for Development (PALDES) Project (Ortega et al. 2009) and are temporally housed in the Museo Paleontológico de Elche, Alicante, Spain. The aim of this paper is to describe and present a tentative identification of these specimens. A new transition model from the plesiomorphic theropod teeth to the highly derived morphology seen in *Spinosaurus* and other spinosaurids is proposed. Finally, we review the palaeobiogeographical hypotheses regarding the origin of Spinosauridae.

Institutional abbreviations.—MUPE HB, Azenak site collection, the Museo Paleontológico de Elche, Alicante, Spain; MUPE TP4, Tadibene Paleosoil 4 site collection, the Museo Paleontológico de Elche, Alicante, Spain.

Other abbreviations.—AL, apical length; CBL, crown base length; CBR, crown base ratio; CBW, crown base width; CDA, crown distal angle; CH, crown height; CHR, crown height ratio; CI, Consistency Index; CMA, crown mesial angle; CVA, Canonical Variate Analyses; DC, distal denticles; DFA, Discriminant Function Analyses; MC mesial denticles; RI, Retention Index.

Geological setting

The geographical and geological settings are the same as those reported for *Spinophorosaurus nigerensis* (Remes et al. 2009). The Azenak (HB) site is located in the Rural Community of Aderbissinat (Agadez, Niger), ~30 km to the north and stratigraphically below the outcrops of the Tegama Group, in a massive to finely laminated red siltstone that belongs to the "Argiles de l'Irhazer" (Irhazer Group). Rauhut and López-Arbarello (2009) favoured a latest Middle Jurassic age for the Tiourarén Formation. The anatomical and phylogenetic context of *Spinophorosaurus* is indeed consistent with such an age (Carrano et al. 2012; Knoll et al. 2012; Mocho et al. 2013).

Material and methods

The material consists of four teeth (Fig. 1). These specimens belong to the Republic of Niger, but are temporarily housed in the Museo Paleontológico de Elche (MUPE, Spain), which is the coordinating institution of the PALDES project. All teeth were found in close association with the remains of *Spinophorosaurus nigerensis*. The crowns are complete enough for several characters to be assessed and metrics to be used. Most denticles are intact, and even basal parts of the crown without enamel have been preserved. The poor preservation shown by these four teeth, compared with the exquisite preservation of *Spinophorosaurus*, suggests they had probably been transported before being finally buried with the sauropod.

Morphometric analysis.—In order to identify the four teeth, non-transformed biometric data from the samples were compared with the dentitions from the dataset of Smith et al. (2005), Smith and Lamanna (2006), and Hendrickx et al. (2015). The dataset contains 995 samples from 59 different taxa: basal Saurischia (*Eoraptor lunensis*),

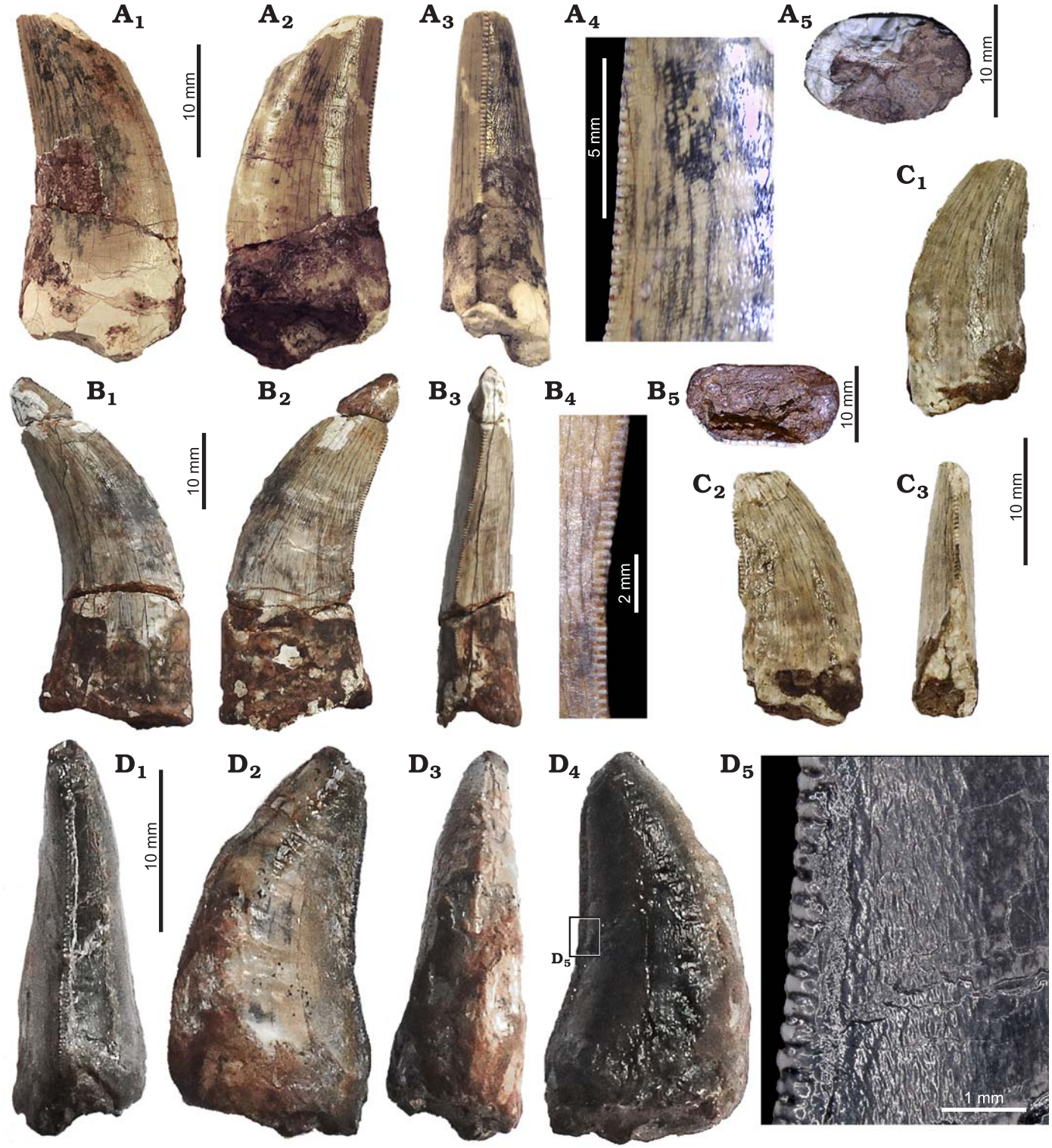

Fig. 1. Theropod teeth from the Middle Jurassic Tegama Group, Agadez, Niger. **A**. MUPE HB-142 in labial (A_1), lingual (A_2), distal (A_3), and basal (A_5) views, close-up (A_4). **B**. MUPE HB-118 in lateral (B_1, B_2), distal (B_3), and basal (B_5) views, close-up (B_4). **C**. MUPE HB-125 in lateral (C_1, C_2) and distal (C_3) views. **D**. Spinosaurid tooth, MUPE HB-87 in distal (D_1), lingual (D_2), mesial (D_3), and labial (D_4) views; close-up view of the labial side (D_5); note the deeply veined enamel surface texture and the shape and size of the distal denticles.

basal Theropoda (*Ischisaurus cattoi*, *Eodromaeus murphi*, *Coelophysis bauri*, *Dilophosaurus wetherilli*, *Liliensternus liliensterni*), Ceratosauria (*Ceratosaurus dentisulcatus*, *Genyodectes serus*, *Berberosaurus liassicus*, *Noasaurus leali*, *Masiakasaurus knopfleri*, *Abelisaurus comahuensis*, *Rugops primus*, *Indosuchus raptorius*, *Majungasaurus crenatissimus*, *Aucasaurus garridoi*, *Skorpiovenator bustingorryi*, *Carnotaurus sastrei*), basal Megalosauroidea

(*Piatnitzkysaurus floresi*), Megalosauridae (*Afrovenator abakensis*, *Duriavenator hesperis*, *Megalosaurus bucklandii*, *Dubreuillosaurus valesdunensis*, *Torvosaurus tanneri*), Spinosauridae (*Baryonyx walkeri*, *Suchomimus tenerensis*, *Irritator challengeri*, *Spinosaurus aegyptiacus*), Allosauroidea (*Allosaurus fragilis*, *Aerosteon riocoloradensis*, *Neovenator salerii*, *Fukuiraptor kitadaniensis*, *Australovenator wintonensis*, a juvenile of *Megaraptor namunhuaiquii*, *Acrocanthosaurus atokensis*, *Eocarcharia dinops*, *Carcharodontosaurus saharicus*, *Giganotosaurus carolinii*, *Mapusaurus roseae*), Tyrannosauroidea (*Eotyrannus lengi*, *Raptorex kriegsteini*, *Alioramus altai*, *Gorgosaurus libratus*, *Daspletosaurus torosus, Albertosaurus sarcophagus*, *Tyrannosaurus rex*), Dromaeosauridae (*Nuthetes destructor*, *Bambiraptor feinbergi*, *Deinonychus antirrhopus*, *Dromaeosaurus albertensis*, *Velociraptor mongoliensis*, *Saurornitholestes langstoni*, *Atrociraptor marshalli*, *Zapsalis abradens*), and Troodontidae (*Troodon formosus*, *Zanabazar junior*, *Pectinodon bakkeri*, *Richardoestesia isosceles*).

We performed a three stepwise Discriminant Function Analyses (DFA), using squared Mahalanobis distances (D2). The DFA used multivariate analyses of variance (MANOVA) with a covariance matrix to determine significant differences between the various genera in the standard, in addition to calculating a canonical vector that maximizes the variation in the data. The canonical functions are analogous to the Principal Components from a PCA. The number of teeth included in each taxon from the database is different, and therefore the canonical vector is influenced by the sample size to maximize the probability of accuracy. Finally, the analysis classified each data case to the genus group to which it is more similar. In the first analysis, we included the entire dataset and variables. When some variables could not be scored, the software used mean values. It only identified correctly 427 samples out of 995 (42.9%). Due to this lack of accuracy, we performed a second DFA, in which the samples with missing values were automatically discarded by the software. The percentage of accuracy improved substantially (90.0%) at the expense of overlooking 536 samples.

A third DFA was performed in which the mesial denticles were not taken into account because 441 teeth from the database lack this variable, and this includes samples of many taxa related initially to the HB teeth (e.g., *Dilophosaurus*, *Ceratosaurus*, *Megalosaurus*, *Dubreuillosaurus*, *Suchomimus*). Removing the mesial denticles from the analysis allowed comparison with these taxa in spite of comparing a structure they lack or that is not preserved. Some taxa were also discarded to improve the accuracy of the analyses as these were, firstly those taxa with autapomorphic or very distinctive characters not present in Agadez crowns. Thus, derived Late Cretaceous tyrannosaurs (*Gorgosaurus*, *Daspletosaurus*, *Albertosaurus*, *Tyrannosaurus*) were removed as their teeth have a clearly different morphology from Agadez crowns, as well as a different biogeographical context (Brusatte et al. 2010). However, tyrannosaurids are still represented in the dataset by *Alioramus*, whose dentition is more similar to that of basal tyrannosauroids (and other tetanurans) than to the thicker teeth of derived tyrannosaurs (Brusatte et al. 2012; Oliver Rauhut, personal communication 2014). Secondly, taxa were excluded either because of the low number of specimens which could cause an statistically uncertain assignment (less than 4; *Ischisaurus*, *Eodromaeus*, *Berberosaurus*, *Noasaurus*, *Rugops*, *Aucasaurus*, *Skorpiovenator*, *Erectopus*, *Piatnitzkysaurus*, *Neovenator*, *Aerosteon*, *Fukuiraptor*, *Eocarcharia*), or due to missing data (*Carnotaurus*, *Australovenator*, *Saurornitholestes*, *Atrociraptor*, *Zapsalis*, *Pectinodon*, *Richardoestesia*). *Irritator* and *Spinosaurus* (each represented by less than 4 teeth) were considered a single taxon, Spinosaurinae, in order to include these taxa in the analyses. The highest percentage of accuracy is 93.5% (Table 1), when the probabilities for a crown to be assigned is equal for all groups, regardless the sample size. To visualize the relative position of each tooth, the scores obtained for the first (X coordinate) and second (Y coordinate) canonical functions of the last analysis (both explaining 84% of variability; Table 2) were translated into a dispersion graph. This delineates the dental morphospace occupied by Agadez teeth and the included taxa according to the variables used. The weight of each variable was measured (Table 3) so as to interpret the meaning of the canonical functions. Statistical analyses were carried out using SPSS Statistics 17.0 (SPSS Inc., Chicago, Illinois) and PAST (Hammer et al. 2001). The metrics and procedure used are based on Smith et al. (2005) and summarized in Fig. 2. All teeth were measured using a digital caliper (Table 4): crown size was assessed through crown base length (CBL), crown base width (CBW), crown height (CH), and apical length (AL). The crown basal shape is given using the crown base ratio (CBR), and the relative height using the crown height ratio (CHR). The apex displacement,

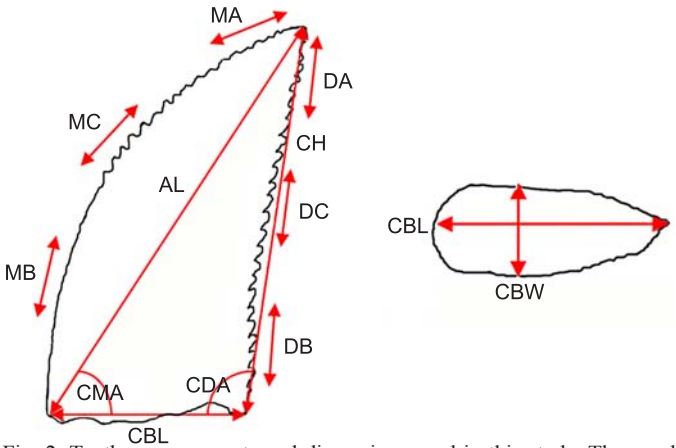

Fig. 2. Tooth measurements and dimensions used in this study. Theropod dental anatomy and variables used, in lateral and basal views (redrawn from Smith et al. 2005). AL, apical length; CA, crown angle; CBL, crown base length; CBR, crown base ratio; CBW, crown base width; CH, crown height; CHR, crown height ratio; DA, distal denticles in the apical section. DB, distal denticles in the basal section. DC, distal denticles in the central section. DSDI, denticle size difference index. MA, mesial denticles in the apical section. MB, mesial denticles in the basal section. MC, mesial denticles in the central section.

or crown curvature, was described using the crown mesial angle (CMA), which was used by Smith et al. (2005), who termed it "CA". It is located between the AL and the CBL. The crown distal angle (CDA), between CH and CBL, was also used. Both are calculated through the use of the law of cosines: C2 = a2 + b2 – 2ab cosθ.

$$\mathrm{CMA} = \arccos\frac{\mathrm{CBL\hat{}2} + \mathrm{AL\hat{}2} - \mathrm{CH\hat{}2}}{2\mathrm{CBL}\cdot\mathrm{AL}}$$

$$\mathrm{CDA} = \arccos\frac{\mathrm{CBL\hat{}2} + \mathrm{CH\hat{}2} - \mathrm{AL\hat{}2}}{2\mathrm{CBL}\cdot\mathrm{CH}}$$

Substituting and solving, in addition, the number of mesial (MC) and distal (DC) denticles at mid-crown, over a distance of 5 mm, was measured. The mesial denticles are not included in the third analysis because several specimens from the dataset in addition to our own samples do not present this character. Thus, it diminishes the accuracy of the analysis as stated in the description of the morphometric analyses.

Discrete qualitative character analyses.—As qualitative characters have recently been considered to be more informative than previously thought (Hendrickx et al. 2015), they have been analyzed in Agadez crowns. In order to compare the HB teeth to the widest possible range of samples, a cluster analysis was performed in PAST using the dentition based characters proposed by Hendrickx and Mateus (2014) and their dataset (see SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app61-SerranoMartinez_etal_SOM.pdf). The paired group algorithm was used and the Jaccard and Simpson indexes were taken as a similarity measurement. All teeth were coded as lateral teeth because distal carinae are not very displaced, and are aligned ~180° with the mesial carinae in all specimens (Smith 2005; Smith et al. 2005). Only lateral teeth characters were used in the cluster analysis. The software employed cannot analyse multistate characters in cluster analyses and, thus, they were not taken into account. Therefore, the most derived state was kept for those taxa with more than one state per character. In addition, a cladistic analysis based on Hendrickx and Mateus (2014) dentition matrix in which the Agadez crowns were included was performed (SOM 2). The software used was TNT (Goloboff et al. 2008), following the protocol procedures of Hendickx and Mateus (2014). The Hendrickx and Mateus (2014) "dentition-only" matrix and supermatrix were used to constrain all major theropod clades (SOM 3). Performing the analysis with all Agadez crowns in both matrices retrieved a basal polytomy, and the analysis was performed with the teeth separated into two morphotypes: MUPE HB-87 (morphotype 1) and MUPE HB-118, MUPE HB-125, and MUPE HB-142 (morphotype 2).

Results

Description.—All measurements and metric variables, including denticle densities, are listed in Table 4.

Table 1. Original grouped cases correctly classified compared to the total number of each taxa based on classification matrix for the discriminant analysis using 31 taxa including the standard dataset provided by Smith et al. (2005), Smith and Lamanna (2006), and Hendrickx et al. (2015).

Taxon	Cases correctly classified	Total number of cases	%
Eoraptor	20	21	95.2
Coelophysis	16	16	100
Liliensternus	7	7	100
Dilophosaurus	4	4	100
Genyodectes	6	7	85.7
Ceratosaurus	12	14	85.7
Masiakasaurus	14	18	77.8
Abelisaurus	4	5	80.0
Indosuchus	10	10	100
Majungasaurus	23	26	88.5
Duriavenator	5	5	100
Megalosaurus	11	12	91.7
Dubreuillosaurus	6	6	100
Torvosaurus	4	4	100
Baryonyx	23	23	100
Suchomimus	14	14	100
Spinosaurinae	4	4	100
Allosaurus	24	29	82.8
Acrocanthosaurus	31	34	91.2
Carcharodontosaurus	14	14	100
Giganotosaurus	7	7	100
Mapusaurus	5	5	100
Megaraptor juv.	4	4	100
Alioramus	15	15	100
Nuthetes	6	9	66.7
Bambiraptor	7	8	87.5
Denonychus	11	11	100
Dromaeosaurus	18	18	100
Velociraptor	18	18	100
Troodon	8	8	100
Zanabazar	7	7	100
Total	358	383	93.5

Table 2. Autovalues and percentage of variance explained by the nine canonical vectors used in the DFA. The canonical functions used in the XY graph account 84.3% of the variance. * the 9 first discriminant canonical functions are used in the analysis.

Function	Autovalue*	% of variance	% accumulated	Canonical correlation
1	12.954	60.8	60.8	0.964
2	5.020	23.6	84.3	0.913
3	1.209	5.7	90.0	0.740
4	0.663	3.1	93.1	0.631
5	0.524	2.5	95.6	0.586
6	0.379	1.8	97.4	0.524
7	0.249	1.2	98.5	0.446
8	0.197	0.9	99.4	0.406
9	0.118	0.6	100.0	0.325

Table 3. Factors of the nine canonical vectors used in the DFA. The first and second vectors are also used in the XY graph that delineates the morphospace of the teeth. Abbreviations: AL, apical length; CBL, crown base length; CBR, crown base ratio; CBW, crown base width; CDA, crown distal angle; CH, crown height; CHR, crown height ratio; CMA, crown mesial angle; DC, distal denticles at mid-crown.

	Standardized canonical discriminant function coefficients								
	1	2	3	4	5	6	7	8	9
CBL	-1.090	1.197	-1.434	0.716	1.433	-1.647	-0.749	0.265	-0.157
CBW	-0.172	0.469	1.051	-0.993	-0.709	-0.982	0.357	0.302	0.283
CH	1.786	0.527	-1.642	-0.332	3.043	-0.426	1.286	-5.132	3.623
AL	-1.114	-1.462	2.177	0.535	-4.093	3.556	-0.531	4.098	-3.677
CBR	-0.141	-0.013	-0.002	1.308	0.632	0.506	-0.018	-0.616	-0.523
CHR	-0.222	0.659	0.055	-2.113	0.746	-1.298	-2.732	-0.055	-1.180
CDA	0.476	-0.403	-0.204	2.331	1.163	0.679	4.193	1.606	2.733
CMA	0.148	-0.901	0.186	3.484	-0.149	1.492	4.459	2.659	3.229
DC	0.619	0.832	-0.064	0.130	-0.083	-0.010	0.069	-0.002	-0.021

Table 4. Morphometric measurements (in mm) and metric variables from the theropod teeth from Niger. Abbreviations: AL, apical length; CA, crown angle; CBL, crown base length; CBR, crown base ratio; CBW, crown base width; CH, crown height; CHR, crown height ratio; DA, distal denticles in the apical section; DB, distal denticles in the basal section; DC, distal denticles in the central section; DSDI, denticle size difference index; MA, mesial denticles in the apical section; MB, mesial denticles in the basal section; MC, mesial denticles in the central section; * estimated values; ?, values unknown that can not be estimated.

Taxon	CBL	CBW	CH	AL	CBR	CHR	CA	MA	MC	MB	DA	DC	DB	DSDI
MUPE HB-87	12.72	8.78	23.82	26.64	0.69	1.87	63.34	17.5	22.5	0	15	17.5	22.5	0.83
MUPE HB-118	18.6	9.87	37.47	46.68	0.53	2.01	49.79	15	11.25	0	12.5	15	21.25	0.94
MUPE HB-125	8.65	5.26	20.26*	23.18*	0.61	2.34	59.81	15	16.25	27.5	15	15	?	1.07
MUPE HB-142	14.12	9.2	31*	34.52*	0.65	2.20	63.83	?	0	0	11.25	12.5	20	?

MUPE HB-142 (Fig. 1A): This is the best preserved tooth as only the tip is broken. It has plesiomorphic theropod tooth traits: labiolingually compressed (ziphodont) and distally curved with distal denticulate carina. The basal cross-section is elliptical. The preserved portion of the mesial margin has an unserrated carina. However, the presence of denticles in the lost apical part cannot be ruled out. The basal half of the mesial margin has a semicircular outline. The distal carina is centrally positioned and has a parabolic curvature, and the denticles are large and closely spaced (2.25 denticles/mm). The apex of the distal denticles is symmetrically convex and the denticles are perpendicular to the distal margin. The crown shows marginal undulations (enamel wrinkles sensu Brusatte et al. 2007) adjacent to the distal carina as well as a slightly braided enamel texture covering its surface.

MUPE HB-118 (Fig. 1B): This is the largest tooth of the collected sample. It was found next to the neurapophysis of a cervico-dorsal vertebra (MUPE HB-10) of the *Spinophorosaurus* holotype. The transition between the root and crown can be distinguished in its most basal portion. This crown is similar in shape to MUPE HB-142. It has an elliptical mid-cross-section with a concavity next to the lingual side of the distal carina. The mesial denticles only extend along the apical third of the total length of the tooth. Most apexes of the mesial denticles are broken and are preserved only in the most apical section, where they have a symmetrically convex shape in lateral view. The distal carina has a sigmoid curvature, and bears small chisel-like denticles (3 denticles/mm). The enamel is ornamented with marginal undulations near both carinae. Weak braided enamel texture is also present over the entire surface.

MUPE HB-125 (Fig. 1C): This is the smallest crown of the sample. Its apex is broken. It is labiolingually compressed and distally curved, but less so than MUPE HB-118 and MUPE HB-142. It was found next to the right pubis of the *Spinophorosaurus* holotype. It has a lenticular cross-section outline at mid-height. The mesial carina extends over three fourths of the total length. The mesial denticles are small (3.25 denticles/mm), apicobasally elongated and asymmetrically convex. The distal denticles are chisel-like in shape and more apically oriented (3 denticles/mm). The enamel is not wrinkled and is only weakly textured.

MUPE HB-87 (Fig. 1D): This specimen was found in the right acetabulum of the *Spinophorosaurus* holotype. It is less curved than the other teeth in lateral view, and has a subcircular cross-section outline (CBR = 0.69). The mesial denticles only occupy the apical part of the carina, and are asymmetrically convex and slightly smaller than the distal ones (3.75 mesial denticles/mm). The distal carina is straight. The distal denticles are chisel shaped, slightly elongated mesiodistally, apically oriented, small and tightly packed (3.5 distal denticles/mm). The entire surface of the tooth shows a deeply veined enamel texture, with apico-basal orientation (Fig. $1D_5$). There are two weak marginal undulations on the labial side of the distal carina.

Morphometric analyses.—In the first and second DFAs, MUPE HB-118, MUPE HB-125, and MUPE HB-142 were assigned to basal tetanurans (*Piatnitzkysaurus*, *Erectopus*, and *Torvosaurus*, respectively) and MUPE HB-87 to *Ber-*

berosaurus. It is remarkable that MUPE HB-87, MUPE HB-118, and MUPE HB-125 were grouped together with taxa that had a small number of samples. On the other hand, the third DFA assigned the teeth to three Jurassic taxa: MUPE HB-87 and MUPE HB-125 were assigned to *Allosaurus*, MUPE HB-118 to *Dilophosaurus*, and MUPE HB-142 to *Megalosaurus*. The first two canonical functions, which were used to delineate an empiric morphospace (Fig. 3), explain 84.3% of the variance. The first canonical function (X axis) has the most important loads from the CBL (negative), CH (positive), and AL (negative) variables (Table 2), so it is interpreted as the lateral outline of the teeth: positive values in the first canonical function implies teeth with a short base and taller and more conical crown, and negative values correspond to teeth with longer base and a larger crown mesial angle. The second canonical function has the most important loads from the CBL (positive), AL (negative), CMA (negative), and DC (positive) variables. It is interpreted as the lateral outline as well as the denticle number: a positive score in the second canonical function implies teeth with longer base, more conical crown, and a higher number of denticles, whereas negative scores correspond to teeth with a shorter base, larger crown mesial angle, and lower number of denticles. The scatter plot (Fig. 3) shows MUPE HB-118 placed near, but outside of, the *Dilophosaurus* morphospace. MUPE HB-118 and MUPE HB-142 fall in an area of the morphospace shared by both *Megalosaurus* and *Allosaurus* (which overlap broadly). MUPE HB-125 does not occupy any morphospace, and lies between the shared morphospace of allosaurids and megalosaurids and that of dromaeosaurids. Finally, MUPE HB-87 falls within the limits of the megalosaurid morphospace, well out of the allosaurid morphospace.

Discrete qualitative character analyses.—All dendrograms obtained from the cluster analysis reveal that teeth of Allosauroidea, Megalosauridae, and Ceratosauria are very similar, as the taxa from those clades are spread and mixed in the analysis (Fig. 4). The teeth of Spinosauridae, Tyrannosauridae, Dromaeosauridae, and Troodontidae are well separated and distributed in different clusters. Cluster analysis of the current samples places all the teeth from Agadez as most similar to the megalosaurids *Dubreuillosaurus* and *Afrovenator*. The addition of teeth of basal, Middle Jurassic, African spinosaurids from Tadibene, Niger (Serrano-Martínez et al. 2015), to the cluster analysis makes MUPE HB-87 group with spinosaurids. The other HB teeth, however, remain associated with *Dubreuillosaurus* and *Afrovenator*, suggesting they most likely belong to a single taxon. The cladistic analysis with all HB crowns included at once yielded a strict consensus tree with all HB teeth grouped together in a clade included in a polytomy within basal ceratosaurs, megalosaurids, allosauroids and tyrannosaurids (SOM: fig. 1) with a CI of 0.334 and a RI of 0.581. When only MUPE HB-87 was included, the strict consensus yielded a better resolved tree, with MUPE HB-87 retrieved as a sister taxon of *Dubreuillosaurus*, as in the cluster analysis, with a CI of 0.341 and a RI of 0.593 (SOM: fig. 2). The analysis with Hendrickx and Mateus' (2014) supermatrix yielded the most robust results when the teeth were split in morphotypes. When only MUPE HB-87 was included, 7 most parsimonious trees were recovered with a CI of 0.567 and a RI of 0.545. The strict consensus found MUPE HB-87 as a sister group of Spinosauridae with a Bremer support of 1 (SOM: fig. 3). When MUPE HB-118, MUPE HB-125, and MUPE HB-142 were all included together in the analysis without MUPE HB-87, 7 most parsimonious trees were retrieved with a CI of 0.565 and a RI of 0.54. The strict consensus retrieved the three HB crowns in a clade nested in Megalosauroidea in a polytomy with Spinosauridae and Megalosauridae, with no changes in the rest of the topology (SOM: fig. 4).

Discussion

Taxonomic affinities of MUPE HB-118, MUPE HB-125, and MUPE HB-142.—The discriminant analysis relates MUPE HB-118 to *Dilophosaurus*, a basal neotheropod from the Lower Jurassic of North America. However, the scatter plot reveals that, although the closest centroid to MUPE HB-118 is that of *Dilophosaurus*, it is out of its morphospace. On the other hand, megalosaurids and allosaurids, which have a larger number of samples, delineate a large morphospace in which MUPE HB-118 falls. Moreover, the *Dilophosaurus* morphospace is entirely contained in the morphospace of megalosaurids and allosaurids, most likely because of the small number of specimens available for this taxon. A larger sample of *Dilophosaurus* should be included to better delineate the morphospace occupied by this theropod and to give it more accuracy and weight in the analysis. In conclusion, this result is not definitive because of the small dataset of the assigned taxon, and thus additional evidence is needed to propose an affinity for this crown. The DFA assigns, with a high percentage of accuracy, MUPE HB-125 to allosaurids, despite it not falling within any morphospace (Fig. 3). Finally, the DFA assigns MUPE HB-142 to Megalosauridae, and in the scatter plot shows that it lies in the middle of the megalosaurid morphospace. These results agree with the first discriminant analyses, which also assigned these teeth to the same basal tetanurans with the exception of MUPE HB-125, which was identified as a basal megalosauroid instead of an allosaurid. Morphometric analyses can group together teeth from different taxa due to their similarities in size, shape, and denticulation patterns of the carinae (Buckley et al. 2010; Richter et al. 2012; Hendrickx et al. 2015). Furthermore, given the superficial morphological and metric similarity between allosauroid and megalosauroid teeth (Fig. 3, SOM: fig. 1; see also Hendrickx et al. 2015), qualitative characters and extrinsic data have to be taken into account. Cluster analyses with discrete qualitative characters reveal all the analysed crowns to be most similar to *Dubreuillosaurus* and *Afrovenator*, which are

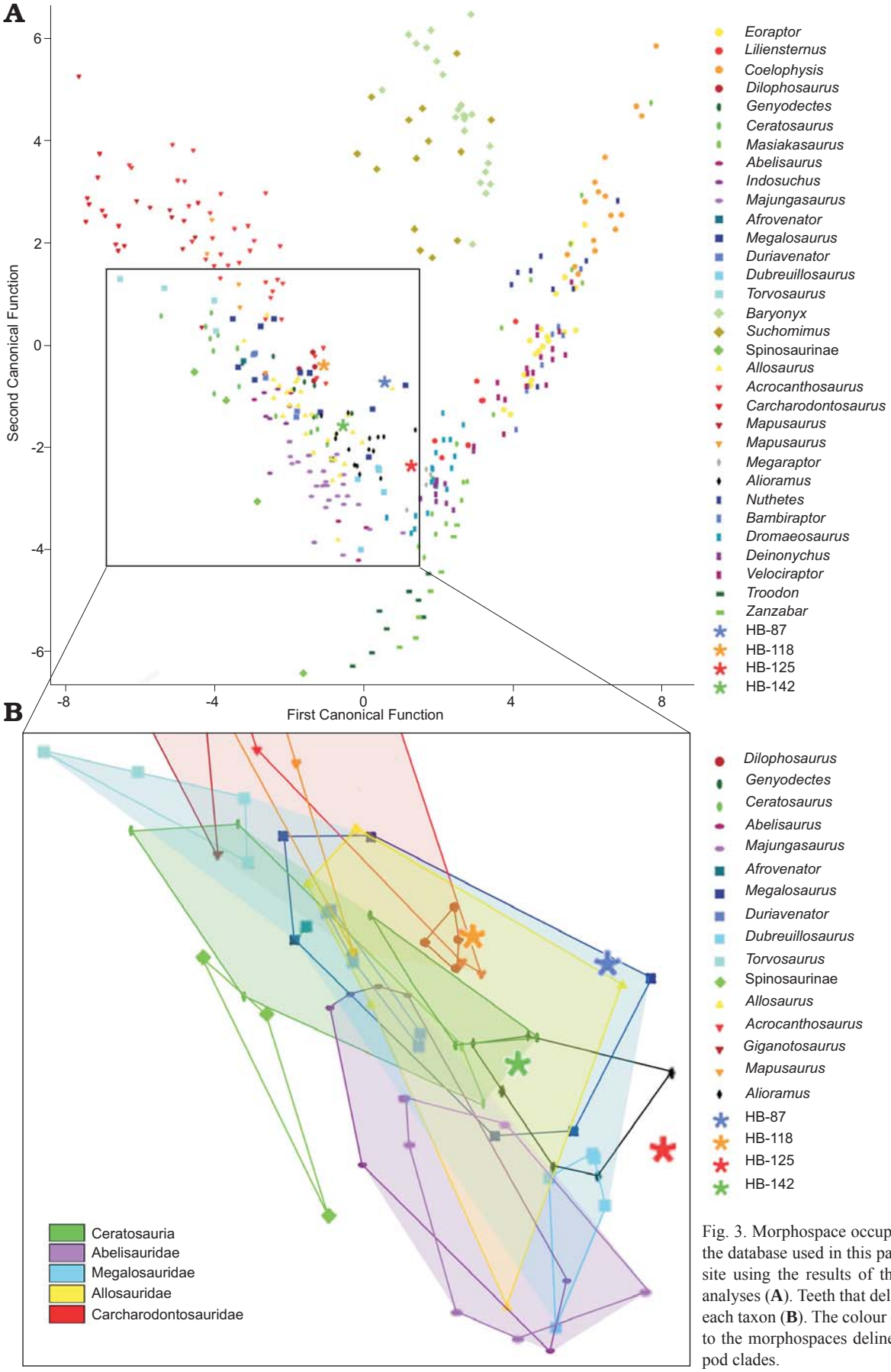

Fig. 3. Morphospace occupied by theropod teeth of the database used in this paper and those of the HB site using the results of the discriminant function analyses (**A**). Teeth that delimit the morphospace of each taxon (**B**). The colour convex hulls correspond to the morphospaces delineated by different theropod clades.

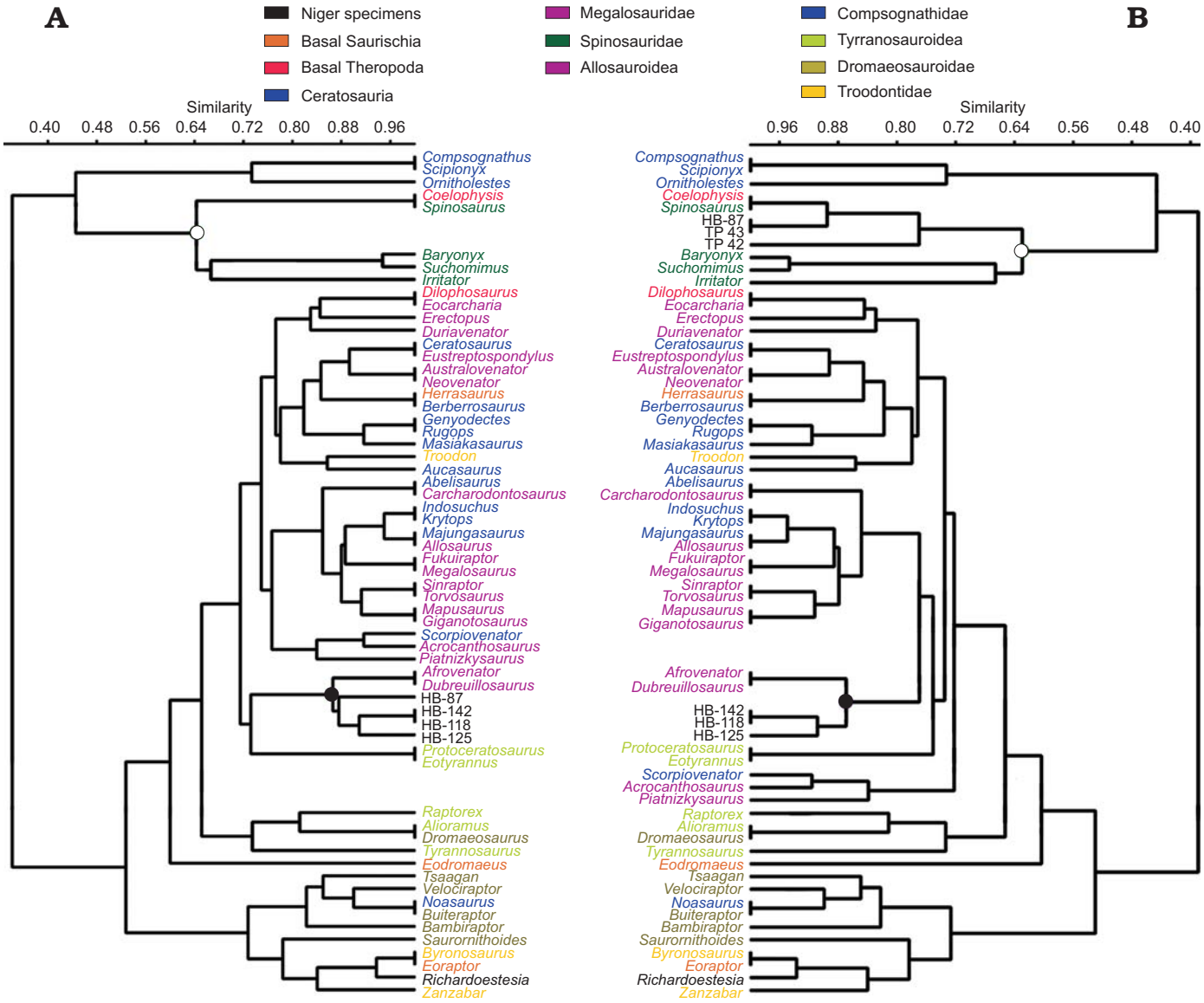

Fig. 4. Dendrogram obtained from the cluster analysis of the theropod teeth. **A**. Database from Hendrickx and Mateus (2014) and the HB site. The characters used were those proposed by Hendrickx and Mateus (2014) for lateral teeth. HB samples are clustered with *Afrovenator* and *Dubreuillosaurus* (black dot). **B**. Database from Hendrickx and Mateus (2014), the specimens from the HB site, and two basal spinosaurid teeth from the Middle Jurassic TP4 site in Niger (Serrano-Martínez et al. 2015). MUPE HB-118, MUPE HB-125, and MUPE HB-142 remain clustered with *Afrovenator* and *Dubreuillosaurus* (black dot), but MUPE HB-87, MUPE TP4-2, and MUPE TP4-3 are clustered with the spinosaurids (white dot).

both megalosaurids (Fig. 4). The teeth are grouped together and constitute the closest cluster to the aforementioned megalosaurids, which suggests that all three teeth might belong to the same taxon. The cladistic analysis also retrieves the three crowns as a clade (SOM: fig. 4), reinforcing the idea that they belong to the same taxon. The slight differences in size and denticle shape can be explained as ontogenetic or positional rather than taxonomic in nature (Smith 2005; Buckley et al. 2010; Hendrickx et al. 2015). Given the absence of Allosauroidea in Gondwana in the Middle Jurassic, as well as the morphological similarity with megalosaurid teeth, and the presence of *Afrovenator* in the Tiourarén Formation (Sereno et al. 1994), MUPE HB-118, MUPE HB-125, and MUPE HB-142 most likely belong to *Afrovenator*.

Taxonomic affinities of MUPE HB-87.—Spinosaurids are characterized by conical teeth with a subcircular cross-section (Charig and Milner 1997; Sereno et al. 1998; Sues et al. 2002), and very numerous and small denticles, 5–9 denticles/mm in *Baryonyx* and *Suchomimus* (Charig and Milner 1986, 1997; database in Smith et al. 2005; Mateus et al. 2011) and 5–13 denticles/mm in isolated teeth (Ruiz-Omeñaca et al. 2005; Hone et al. 2010). Unserrated carinae have also been noted in *Spinosaurus* and *Irritator* (Stromer 1915; Sues et al. 2002). The appearance of low subconical, slightly recurved crowns is also noted in basal spinosaurid teeth (CBR = 0.69 and CMA = 56.66° in MUPE TP4-2; Serrano-Martínez et al. 2015) and some *Suchomimus* teeth (CBR = 0.65 and a pronounced curvature in UC G73-3; Christophe Hendrickx,

personal communication 2015). The DC of MUPE HB-87 is not very high (3.5 denticles/mm), but is higher than in most ceratosaurs, non-spinosaurid basal tetanurans, and tyrannosauroids. Reduction in the number of denticles is also noted in basal spinosaurids (2−4 denticles/mm in some spinosaurid teeth from the Middle Jurassic of Niger (Serrano-Martínez et al. 2015) and in the putative spinosaurid *Ostafrikasaurus*) and considered it one of the most significant features of spinosaurid dental evolution. The presence of a mesial carina restricted to the apical part of the tooth is also noteworthy. Hendrickx et al. (2015) cite the mesial carina reaching the cervix as present in all spinosaurids. However, some teeth referred to Spinosauridae from the Lower Cretaceous of Spain (CMP3-760; Canudo et al. 2008: fig. 6) have mesial carinae that clearly do not reach the cervix. The mesial carinae of MUPE HB-87, which does not reach the cervix, would not rule out an affinity with spinosaurids. Other characteristic features observed by Buffetaut (2011) are changes in the shape of the teeth, with basal spinosaurids not exhibiting as conical crowns as the more derived taxa. As for the enamel ornamentation, marginal undulations are homoplastic structures that had appeared in many theropod groups (e.g., Abelisauroidea, Megalosauroidea including Spinosauridae, Allosauridae, Carcharodontosauridae, Tyrannosauroidea, Dromaeosauridae; Brusatte et al. 2007; Canale et al. 2009; Hendrickx and Mateus 2014). However, the presence of deeply veined enamel surface texture is a character that had only previously been found in Spinosauridae (Stromer 1915; Charig and Milner 1986; Sereno et al. 1998; Canudo et al. 2008; Hasegawa et al. 2010; Buffetaut 2011; Hendrickx and Mateus 2014). Spinosaurid teeth show another type of synapomorphic ornamentation: apico-basal ridges (flutes sensu Hendrickx and Mateus 2014). The presence of deeply veined enamel surface texture together with the absence of longitudinal ridges in MUPE HB-87 reinforces the hypothesis of the independence of the two ornamentation characters (Serrano-Martinez et al. 2015). Deeply veined enamel texture would be a plesiomorphic trait for spinosaurids, whereas flutes would have appeared in spinosaurids more derived than MUPE HB-87.

The first two discriminant analyses assigned MUPE HB-87 to *Berberosaurus*, and the third one to the basal tetanuran *Allosaurus*. In the scatter plot, it is located in the upper limit of megalosaurids and separate from the allosaurid morphospace. It is notable that it is placed below the spinosaurids *Baryonyx* and *Suchomimus*. That is, it has a higher score in the second canonical function, which implies a more conical crown than in most basal tetanurans but lower than in baryonychine spinosaurids (*Suchomimus* and *Baryonyx*). As stated in the results, the number of denticles has an important role in scoring the second Canonical Function (Y axis): MUPE HB-87 has numerous denticles, more than most basal tetanurans, but not as many as baryonychines, in addition to an intermediate crown mesial angle. This position in the scatter plot may be because MUPE HB-87 shows morphometric tooth characters between derived spinosaurids and

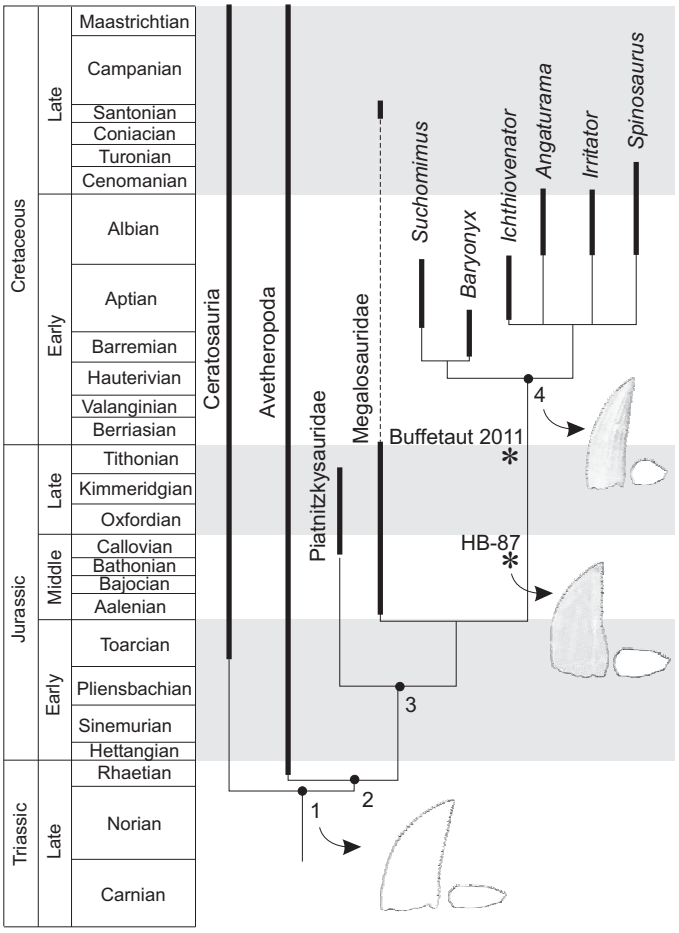

Fig. 5. Time-calibrated phylogeny of spinosaurids and related theropods. Time-calibrated cladogram elaborated after Carrano et al. (2012) and Allain (2014). The asterisks mark the place of the three basal spinosaurid forms represented only by teeth (Buffetaut et al. 2011; this article). The proposed transition from a plesiomorphic theropod tooth (node 1 and earlier) to a highly derived spinosaurid tooth (node 4) would include a transitional state (represented by MUPE HB-87). 1, Averostra; 2, Tetanurae; 3, Megalosauroidea; 4, Spinosauridae.

basal tetanurans. Thus, MUPE HB-87 appears as a transitional form between the typical teeth of spinosaurids and those of their basal tetanuran ancestors (Fig. 5).

The similarities of MUPE HB-87 retrieved in the cluster analysis (Fig. 4) show that it is most similar to basal spinosaurid teeth from a site in the Tadibene area, which belongs to upper strata of the Irhazer group (Serrano-Martínez et al. 2015). When Tadibene teeth are excluded from the analysis, the most similar teeth to MUPE HB-87 are those of *Afrovenator* and *Dubreuillosaurus*, which are both megalosaurids. The cladistic analyses show similar results. Using the teeth-only matrix (SOM: fig. 2), MUPE HB-87 is retrieved as a megalosaurid (as the sister taxon of *Dubreuillosaurus*). However, when using a supermatrix with dental, other cranial and postcranial characters for the other taxa, MUPE HB-87 is retrieved as the sister group of Spinosauridae (SOM: fig. 3).

In summary, all the analyses performed consistently find megalosauroid affinities for MUPE HB-87, sometimes as a

megalosaurid very close to the rest of HB teeth and otherwise as a spinosaurid. This would allow for three different hypothesis: (i) MUPE HB-87 belongs to a basal megalosaurid, the same taxon than the rest of the HB teeth; (ii) MUPE HB-87 belongs to a different Megalosauroidea from the stem group Spinosauridae; (iii) MUPE HB-87 belongs to a member of the stem group Megalosauroidea. In each case, MUPE HB-87 would belong to a basal taxon. Considering its basal condition and its limited data (it is an isolated tooth), it is not surprising that some analyses find it more related to megalosaurids and other analyses find it more related to spinosaurids.

MUPE HB-142 and MUPE HB-87 have similar measurements, CBR values and non-displaced carinae which would indicate a similar location in the jaws if they belonged to the same taxon. However, MUPE HB-87 has distal denticles that are different in morphology, size as well as enamel texture being more pronounced.

Given these results, and considering that MUPE HB-87 shares several qualitative characters with basal Spinosauridae (MUPE TP4-2 and TP4-3) and derived Spinosauridae (*Suchomimus*) not present in other HB teeth, its referral to a member of the stem group Spinosauridae is proposed. If confirmed, this would be the oldest representative of this group, predating the specimens recently reported by Serrano-Martínez et al. (2015).

Implications on the paleobiogeography of Spinosauridae.—Based on the fossil record, Spinosauridae is mainly a Cretaceous clade, yet its sister group, Megalosauridae, is already known from the Middle Jurassic (Carrano et al. 2012). The existence of Jurassic spinosaurids has recently been proposed on the basis of questionable isolated teeth from the Upper Jurassic of Tanzania (Buffetaut 2008, 2011; Rauhut 2011), two isolated teeth from the Middle Jurassic of Niger (Serrano-Martínez et al. 2015) and, probably, MUPE HB-87.

As all these aforementioned Jurassic remains are from Africa, a Gondwanan origin of Spinosauridae is plausible. This hypothesis agrees with the record of an Australian spinosaurid (Barrett et al. 2011). The Australian landmass (as well as the Indian and the Antarctic) was isolated from the rest of Gondwana in the Late Jurassic (Fig. 6). Early spinosaurids may have dispersed to that landmass before Gondwana broke up (Buffetaut 2011; Allain et al. 2012). After the first appearance of spinosaurids in Gondwana, their distribution becomes unclear. Spinosaurids had a worldwide distribution by the Early Cretaceous (Fig. 6), with remains found in Africa, South America, Asia, Australia, and Europe (Bertin 2010). It is hypothesized that the opening of the Tethys Sea allowed baryonychines to evolve in Laurasia and spinosaurines in Africa (Sereno et al.1998), and from there they were able to spread to South America (Machado and Kellner 2005). Mateus et al. (2011) considered that the appearance of similar baryonychines in Africa and Europe suggests a migration between higher and lower latitudes, and dispersal, rather than migration, would be a more likely explanation for their distribution. This displacement has usually been considered from North to South (Buffetaut and Ouaja 2002; Machado and Kellner 2005; Ruiz-Omeñaca et al. 2005), but a Gondwanan origin for the clade, and the presence of both spinosaurines and baryonychines in the Iberian Peninsula and, possibly, in Asia (Bertin 2010; Hasegawa et al. 2010; Hone et al. 2010; Allain et al. 2012; Alonso and Canudo 2015) makes any inference about the direction of the dispersal uncertain or, at least, more complex than previously thought.

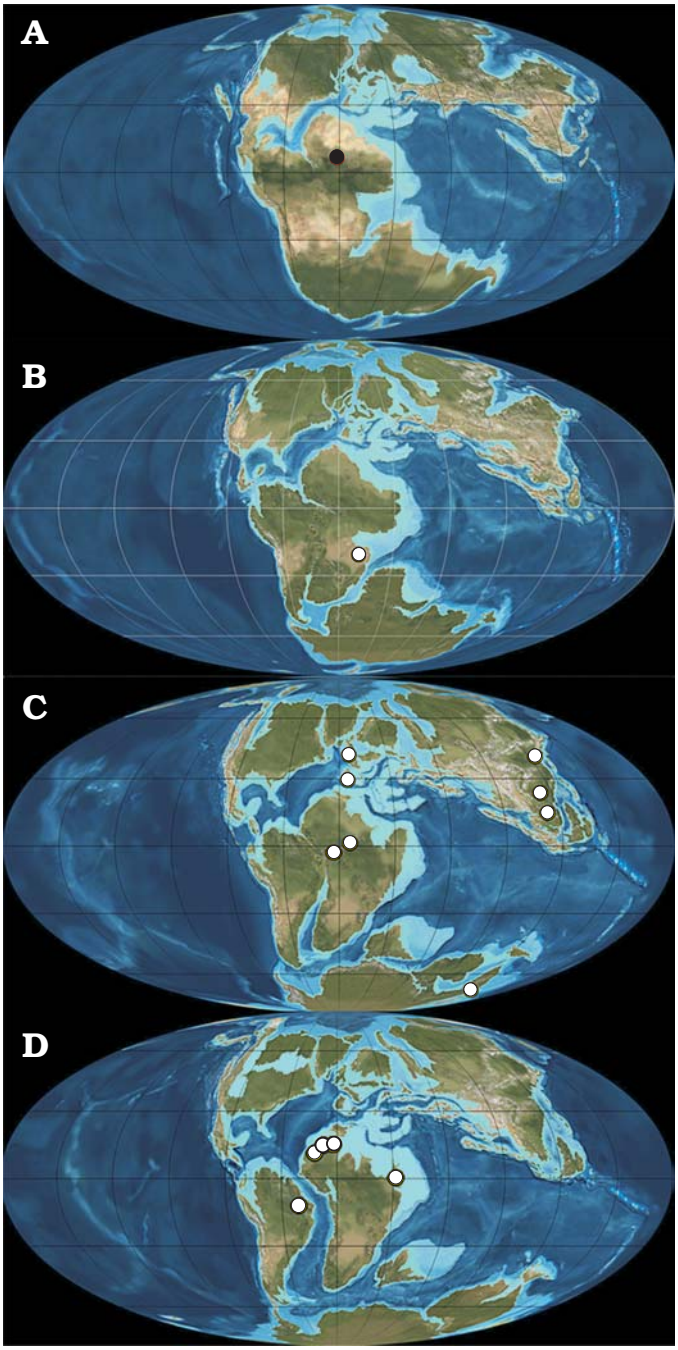

Fig. 6. Generalized palaeogeographic locations of spinosaurids (white) and the specimen of HB site (black), through time from Bajocian–Bathonian (**A**), Tithonian (**B**), Barremian−Aptian (**C**), and Albian−Cenomanian (**D**). Courtesy of Ron Blakey (http://jan.ucc.nau.edu/~rcb7/mollglobe.html), modified and actualized after Bertin (2010).

Conclusions

The current study suggests the presence of at least two theropod taxa in the Middle Jurassic of the Rural Community of Aderbissinat (Agadez, Niger). The first taxon is represented by three ziphodont teeth. Biometrical discriminant, cluster, and cladistic analyses support their assignment to a megalosaurid, most likely *Afrovenator*. The other taxon, which is represented by an isolated tooth, might be the earliest known member of the stem group Spinosauridae. This crown shows an uncommon morphology. It has minute denticles and deeply veined enamel surface texture like other spinosaurid teeth, and its section and curvature falls within the range of described spinosaurids. However, it lacks enamel flutes like the teeth of most non-spinosaurid tetanurans. This may indicate that the two ornamentations present together in derived spinosaurid teeth evolved separately; the deeply veined enamel surface texture would have appeared in the stem group of spinosaurids, and the flutes in more derived members of the clade. Finally, this tooth supports the hypothesis of a Gondwanan Middle Jurassic origin for Spinosauridae.

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